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Notes on Xerophytic Ferns*

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The material given in the following paper has been collected through some seventeen years of work with various xerophytic ferns. There is in this presentation very little that is actually new. It is rather an attempt to bring together related information collected through this period of years and to add to that some final findings and general considerations.

By most students of ferns, the prothallia have been thought of as very delicate structures readily succumbing to drought, extremes of temperatures and other unsatisfactory conditions. Before 1912 very little work indeed had been done on the ability of fern prothallia to survive periods of water shortage or actual desiccation. Before that time some German students had published papers dealing with the ability of certain mosses to live through long periods with a reduced water supply. Papers had also been published describing the ability of certain moss and fern spores to live through periods of several years in normally dry atmosphere. It was also well known that seeds and some other structures of higher plants could revive and continue growth and other activities after several years of dry storage. It is true that Goebel had described before the above date

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special tuberous outgrowths produced by the prothallium of *Anogramme chaerophylla* which when covered with soil might survive dry seasons and continue growth when conditions became favorable. Campbell had also called attention to the survival through extended periods of drought of the prothallia of *Gymnogramme triangularis* in the neighborhood of Stanford, California. He also had recorded the fact that a culture of these fern plants had survived exposure to dry air in the laboratory all summer. No study had been undertaken, however, to determine how long prothallia might live under such conditions or to find what changes would result from such treatment.

In 1912 while the writer was making a careful study of the life history of the little Walking Fern, *Camptosorus rhizophyllus,* he found that the prothallia of this plant were to an unexpected degree able to withstand exposure to desiccating conditions. A further study of this particular plant and of the Ebony Spleenwort, *Asplenium platyneuron,* brought out this peculiar characteristic even more definitely. It was found that these prothallia were able to survive exposure to repeated periods of three or four weeks of such drought as may occur under natural conditions.

In 1920–1923 similar though more extensive studies were made of the prothallia of *Cheilanthes gracillima,* a small fern found growing over a wide area of Washington, but limited rather closely to exposed rocky regions. Spore cultures of this fern were grown and after some of the prothallia had reached maturity were exposed to conditions of desiccation. Some were exposed to the dry air of the laboratory. Portions of other cultures were placed in desiccators over anhydrous calcium chloride and over anhydrous phosphoric acid. Plants exposed to the normal dry atmosphere of the laboratory from April 1, 1922, to September 21, 1922 (nearly sixteen weeks), showed almost 100 per cent recovery. Plants which had been exposed to the dry air of the laboratory for six months and then placed in desiccators, as indicated above, for thirteen weeks showed almost complete recovery after the application of water. In these cases final survival was proven by placing the cultures or portions of cultures under proper growth conditions and determining the percentage of survival after the plants had ample time to continue normal growth.

In 1924 and 1925 similar studies were made on two forms of Purple Cliff Brake, *Pellaea atropurpurea* and *Pellaea glabella*. Cultures of these plants remained air dry in the laboratory from June 5, 1924, to March 24, 1925, a period of nine months and twenty days. The prothallia were mature, some of them showing young sporophytes. After the application of water to these cultures fully seventy-five per cent of the plants showed recovery and normal growth. After eighteen and a half months of desiccation a considerable number of whole plants recovered and small active areas were found in many others. A further experiment was in progress at the time the report of this work was published. At this time the final results of that experiment will be given. One culture in a six-inch clay saucer had been allowed to become air dry in the greenhouse and then placed in a dark but dry and well ventilated cupboard. On June 18, 1929, exactly five years later, this culture was removed and was put under satisfactory conditions for growth. It at once became evident that most of the plants were dead. However, a considerable number, perhaps five per cent of the total, showed either complete recovery as individuals or showed masses of living cells.

A series of experiments was carried on to determine the exact amount of water, if any, remaining in these plants after long periods of desiccation. Small portions of soil covered with the dry prothallia were removed from cultures that had remained air dry in the laboratory for eleven months. These were very carefully weighed and then were placed in a drying oven with a temperature of from 90° to 110° C. for five hours. The masses of material used were small, so small indeed that there could be little doubt but that any residual water would be removed by this treatment. The actual loss as determined by careful weighing before and after this drying varied between four- and five-hundredths of one per cent of the total weight. Similar portions taken from the same cultures and put under suitable conditions showed a high percentage of survival and later growth of the prothallia.

In 1924 and 1925 similar experiments were carried out with prothallia of the western Polypody, *Polpodium vulgare* var. *occidentale*. It should be remembered that while this fern does not grow in arid regions, it does grow in mats of moss on logs, stumps and sometimes high above the ground on branches of trees. This habitat exposes the plants to periods of drought each year, periods that may extend over three months or more. Specimens have been noted growing on the branches of *Quercus Garryana* at the home of W. N. Suksdorf, at Bingen, Washington, where there is but a trace of rainfall from May to September.

Spores of this plant were grown in cultures that produced normal mature plants in twelve weeks. These were allowed to remain air dry in the laboratory from July 15 to October 1. After the application of water, there was almost 100 per cent revival and continued growth. Both prothallia and young sporophytes survived the season of drought.

Surely fern prothallia have no means of preventing the loss of water. They are for the most part but one cell in thickness, and the cell walls show but little evidence of cutinization. Careful examination of desiccated specimens shows that they have lost all water. The protoplasm is hard and horny, and vacuolar cavities have disappeared through the total collapse of the walls.

A very striking feature in the development of these xerophytic fern prothallia is their tendency toward vegetative propagation. While this tendency is shown by all the xerophytic forms studied, it is brought about by different methods in the different species. Old prothallia of *Camptosorus* and *Cheilanthes* which have undergone long or repeated short periods of desiccation and have then been placed under favorable conditions for growth often show a great part of the body tissue dead, although the margins show green and active cell groups. These marginal cells develop into growths in every way similar to primary prothallia. In time they may be entirely separated through the death and decay of the older tissue and then continue their life and growth as independent plants. That this becomes an important factor in increasing the number of plants as well as in continuing their growth is shown by the fact that more than a dozen such proliferations have been found on a single prothallium. In the *Pellaeas* the development of proliferations is chiefly brought about through the activity of more or less completely isolated groups of cells scattered at random through the bodies of prothallia that have shown injury at the end of periods of desiccation. Only occasionally are these masses marginal except such as are located in the apical sinus. The group of eight or ten cells may appear green and active in the central part of a prothallium that is otherwise dead. These cells may produce a projection extending directly from the surface of the old prothallium. This projection will develop as a normal prothallium or it may branch repeatedly, each branch developing as a normal prothallium.

Somewhat closely related to the vegetative propagation just described is the development of apogamous embryos by some of these ferns. As far as the writer's studies have shown the two species of *Pellaea* mentioned produced sporophytes apogamously only. Normal archegonia have not been found although antheridia were formed quite regularly. Apogamous embryos were formed freely from living tissue near the apical sinus or from other marginal masses of cells. It is not unusual to find two or more such embryos on one prothallium.

In *Asplenium platyneuron* there has been found an extreme sensitiveness to variations in light intensity which also leads to the production of various proliferation and subsequent vegetative propagation. With a slight reduction in light intensity these prothallia will produce greatly elongated cells, several such cells appearing on the margin of an individual prothallium. With a slight increase in light intensity through a period of two or three days, each of these elongated cells will produce at its tip a group of cells resembling in every way a normal young prothallium. In due time, as a matter of fact, these groups do develop into normal prothallia. Alternating periods of bright days and dull days may thus produce from a single spore several independent plants.

There is always a question as to the relation between such laboratory experiments and the conditions found in nature. The following data may show that the results of the experimental work in this case are closely paralleled by actual findings in the field.

Prothallia of *Asplenium platyneuron* and of *Camptosorus rhizophyllus* have been found growing in the field in spring and summer, the former on soil in exposed locations, the latter protected by the mats of moss where this fern is commonly found growing. The size and condition of these prothallia indicated clearly that they had grown through one full summer season at least, and that they had lived through the following winter. Mature prothallia of *Cheilanthes* were found in abundance on exposed soil in such condition as to indicate without doubt that they had lived through at least one full summer and the succeeding winter. These old prothallia found in the field showed in many cases the proliferations and other peculiar vegetative growth which had previously been found in controlled cultures. There can be but little doubt as to the importance of the combination of the ability to survive desiccation and extreme temperature changes together with the unusual capacity for vegetative propagation in the preservation of these species of ferns.

One very striking feature of *Cheilanthes gracillima* should be mentioned in this connection. The pinnules of this fern are covered with a dense tomentum below, and when dry their margins are rolled inward, forming a compact, nearly cylindrical body. This is the normal summer condition and appearance of fronds that have matured in the spring. If such fronds are placed in a moist chamber, the pinnule margins unroll, and spores are scattered in abundance. The fronds may be allowed to become alternately dry and moist several times in succession with the scattering of spores with each new moistening. That this fits into the conditions under which the plants grow is shown clearly by close field observation. The spores are matured in April or May.

The fronds became dry and remain so through the summer. With the coming of fall rains they relax and the spores are scattered. The alternating damp and dry days of October furnish ideal conditions for the scattering of spores and for the growth of prothallia.

It seems very probable that careful study of the development of other ferns growing in areas where extreme drought prevails through at least a part of the year will show many other species with adaptive features similar to those noted above.

This material, in practically its present form, was presented at the summer meeting of the Ecological Society of America at Eugene, Oregon, June 20, 1930. A list of titles of previous publications is given for the benefit of such as may care to know more details of the work.

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Notes on a New Jersey Fern Garden—II.

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PELLAEA ATROPURPUREA

Purple Cliff Brake suggests to me the limestone ridges of northwestern New Jersey. On a fern hunting expedition in 1928 to the vicinity of Newton this cliff brake was found in considerable abundance. Walking fern was plentiful in places and rue-spleenwort not uncommon, but I was chiefly interested in the cliff brake as the others were already in my garden and there was a little limestone cliff, or rather part limestone, waiting for new tenants.

Rue Spleenwort (*Asplenium Ruta-muraria*) was found the year before on rock ledges near Cranberry Lake. The ledges were not limestone and the plants were all small, hardly over an inch in length. A few were brought home and planted on the miniature cliff; they are still growing but are no larger than when found. Near Newton *Ruta-muraria* was found on limestone rocks, often in company with Purple Cliff Brake and Maidenhair Spleenwort and perhaps all three would be crowding each other for the same foothold. In one tiny crevice was found three little fronds, one of each kind, crowded together. The group was carefully lifted and